This is a digital copy of a book that was preserved for generations on library shelves before it was carefully scanned by Google as part of a project to make the world's books discoverable online.

It has survived long enough for the copyright to expire and the book to enter the public domain. A public domain book is one that was never subject to copyright or whose legal copyright term has expired. Whether a book is in the public domain may vary country to country. Public domain books are our gateways to the past, representing a wealth of history, culture and knowledge that's often difficult to discover.

Marks, notations and other marginalia present in the original volume will appear in this file - a reminder of this book's long journey from the publisher to a library and finally to you.

Usage guidelines

Google is proud to partner with libraries to digitize public domain materials and make them widely accessible. Public domain books belong to the public and we are merely their custodians. Nevertheless, this work is expensive, so in order to keep providing this resource, we have taken steps to prevent abuse by commercial parties, including placing technical restrictions on automated querying.

We also ask that you:

+ *Make non-commercial use of the files* We designed Google Book Search for use by individuals, and we request that you use these files for personal, non-commercial purposes.

+ *Refrain from automated querying* Do not send automated queries of any sort to Google's system: If you are conducting research on machine translation, optical character recognition or other areas where access to a large amount of text is helpful, please contact us. We encourage the use of public domain materials for these purposes and may be able to help.

+ *Maintain attribution* The Google "watermark" you see on each file is essential for informing people about this project and helping them find additional materials through Google Book Search. Please do not remove it.

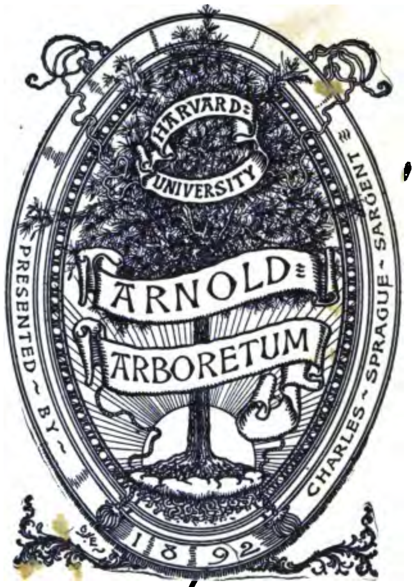
+ *Keep it legal* Whatever your use, remember that you are responsible for ensuring that what you are doing is legal. Do not assume that just because we believe a book is in the public domain for users in the United States, that the work is also in the public domain for users in other countries. Whether a book is still in copyright varies from country to country, and we can't offer guidance on whether any specific use of any specific book is allowed. Please do not assume that a book's appearance in Google Book Search means it can be used in any manner anywhere in the world. Copyright infringement liability can be quite severe.

About Google Book Search

Google's mission is to organize the world's information and to make it universally accessible and useful. Google Book Search helps readers discover the world's books while helping authors and publishers reach new audiences. You can search through the full text of this book on the web at `http://books.google.com/`

Tbac
W58

JP



~~DEPOSITED AT THE
HARVARD FOREST
194[illegible]~~

RETURNED TO J. P.
MARCH, 1967

With the writer's regards A3

REPRINTED FROM THE BOTANICAL GAZETTE, VOL. XXXI, MAY, 1901

THE GENETIC DEVELOPMENT OF THE FORESTS OF NORTHERN MICHIGAN; A STUDY IN PHYSIOGRAPHIC ECOLOGY

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.
XXVII

H. N. WHITFORD

CHICAGO
The University of Chicago Press
1901

VOLUME XXXI NUMBER 5

BOTANICAL GAZETTE

MAY, 1901

THE GENETIC DEVELOPMENT OF THE FORESTS OF NORTHERN MICHIGAN; A STUDY IN PHYSIOGRAPHIC ECOLOGY.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXVII.

HARRY NICHOLS WHITFORD.

(WITH EIGHTEEN FIGURES)

PORTIONS of the summers of 1898, 1899, and 1900 were spent by the writer in studying physiographic ecology at several points in northern Michigan. The work of the first two summers was under the personal direction of Dr. H. C. Cowles, to whom the writer is indebted for many valuable suggestions. Indeed, the work set forth in the present paper is little more than the testing and working out in detail the ideas on physiographic ecology developed by Dr. Cowles in his lectures at The University of Chicago and in his published papers. Credit is due Mr. W. B. McCallum for the photographs used to illustrate this article, with the exception of *figs. 1* and *4*, which were obtained by Mr. E. N. Transeau.

It should be clearly understood that the conclusions reached are based mainly on observations and are presented tentatively. They are published in the hope that they may be thoroughly tested by other observers, and if necessary modified or discarded altogether. It is the writer's belief that only along lines similar to those advocated here can the problems of forest distribution be successfully solved.

I. FACTORS.

The factors to be taken into account in attempting to explain the relations that exist in different plant associations are so complex that it will be well to consider them in detail. Since the object of this paper is to answer some of the questions involved in the development of forests, special emphasis will be laid upon those factors which appear to be related to tree growth. In order to understand the distribution of trees the subject must be approached from both the negative and affirmative standpoints. In other words, the question is, why are there forests on certain physiographic formations and none on those which lie close by? Also within the forest itself there predominates now one and now another tree type. In some places the coniferous forest is prominent, in others the maple-beech-hemlock type is the chief feature. Indeed, if enough regions are studied an indefinite number of combinations may be observed. Thus not only must the presence or absence of trees be explained, but also where trees are present a reason must be given for the dominance of any particular kind of forest. If these questions can be answered satisfactorily, some light will be thrown on the origin and development of forests. In the answer three sets of factors are involved, climatic, ecological, and historical.

A. **Climatic factors.** The greater part of the eastern half of the United States is a potential forest. Here the two great climatic factors, *temperature* and *moisture*, are favorable to the development of forest trees. When a climate makes possible the development of any predominant type of vegetation that type is called a *climatic formation.*[1] To be specific, the eastern half of the United States has a *forest formation.* But if a bird's-eye view of any portion of this formation be obtained, there will be found within it groups of other plant types. These are designated by Warming[2] *plant societies.* Within this vast forest formation there are prairie, beach, dune, heath, swamp, and other plant societies; also the forest itself may be divided into a number of different forest societies. This leads naturally to the consideration of those factors that make up the plant society conditions.

---

[1] SCHIMPER, A. F. W.: Pflanzengeographie auf physiologischer Grundlage. 1898.

[2] WARMING, E.: Plantesamfund. 1895. German edition, translated by Knoblauch. 1896.

B. **Ecological factors.** For convenience this set of factors may be divided into edaphic, atmospheric, hydrodynamic, and biotic.

Edaphic factors. Schimper[3] has regarded the soil and its properties so important that he has given the name *edaphic formations* to those *societies* which owe their existence to the peculiarities of the soil. More than any other form of vegetation trees need a firm anchorage medium, and hence a deep soil. Since the roots are the absorbing as well as the holdfast organs, the water content of the soil is important. Warming's classification of plant societies[4] into xerophytic, hydrophytic, and mesophytic is based upon the amount of water in the soil. More plant societies doubtless owe their characteristic physiognomies to the amount and condition of the water in the soil than to any other one factor. Since trees present a greater transpiration surface than other forms of plants they must occupy those positions where there is sufficient water to maintain the transpiration current. This excludes them from those regions where the water content of the soil approaches the minimum; a stagnant condition of soil water is likewise injurious to trees. Probably here the exclusion of air and the presence of humic acids prevent the healthy growth and activity of the root system. In order that the forest condition may be obtained, therefore, the soil must be well drained, as well as watered.

The physical properties of the soil play an important rôle, for upon them depends the capacity of the soil to hold water. The water-holding properties of the different kinds of soil are too well known to need treatment here. The heat-absorbing and heat-retaining qualities of soils must be taken into account, for they often determine the presence or absence of certain plants.

---

[3] *Op. cit.*

[4] *Op. cit.*

Again, the soil furnishes the plant certain organic and inorganic compounds, and hence its chemical properties should be considered. As a rule, inorganic salts are present in sufficient quantities in the soil; indeed in salt marshes the presence of too great a quantity of salt in the water excludes trees, except in a few instances. Soils are more often deficient in organic compounds. Organic decay, since it furnishes most of the available nitrates, is of great importance. The amount of *humus* is so essential that it often determines the character of a forest, not only in furnishing the nitrogen to the plants, but also in ameliorating the physical properties of the soil. Nitrifying bacteria are necessary for the conversion of organic matter into nitrates, and if these are excluded the processes of organic decay discontinue, and consequently a condition like that present in sphagnum swamps is developed. Here, generally speaking, trees are excluded, except a few characteristic species.

We must look to the soil factors for an explanation of our most characteristic plant societies. There must be a soil. The water in the soil must be sufficient. The soil must be aerated. The amount of organic and inorganic compounds must not be too great or too little, and usually the soil must contain bacteria or other fungi for organic decay. If all these conditions are present in the right proportions, the soil is capable of supporting a luxuriant tree growth.

ATMOSPHERIC FACTORS. By atmospheric factors are meant those which influence the aerial parts of plants. They include radiant energy in the form of *heat* and *light*, and also the influence of *wind*. Of these light is the most important. The tree by virtue of its many planes of plagiotropic branches gives a greater surface on which the light may fall than is found in any other plant form. Principally because it has worked out this successful light relation, it is ecologically the culminating type of plant body. Once a dense forest is established, all forms of low vegetation, except those species that have special shade adaptations, are driven out. Attention has already been called to the necessity of heat as a climatic factor. Heat may also be an ecological factor. In exposed situations the water and humus contents of the soil may be dried out. For example, a forest may be cleared and thus exposed to the sun's rays to such an extent that the soil factors will be changed considerably. It is obvious that it is difficult to separate the light and heat factors. While it is a benefit for a plant to get as much light as possible up to a certain point, along with the light the plant may absorb too much heat.

The carbon dioxid content of the air is so constant that it plays little or no part as an ecological factor. Those plants nearest the ground are slightly favored by the greater amount of carbon dioxid in the lowest layers of the atmosphere. The effect of winds on trees, however, is often pronounced in exposed situations. Besides destroying trees the wind may injure them to such an extent that in the struggle with disease and with other trees they will be the first to succumb. The wind is of great importance also in that it causes excessive transpiration. The effect of wind on seed distribution is so pronounced that, other things being equal, those plants whose seeds are most easily distributed will stand the best chance in a given area. In conclusion, therefore, the atmospheric factors of light, heat, and wind must be taken into account in trying to explain the presence or absence of certain plant societies.

HYDRODYNAMIC FACTORS. The term hydrodynamic is used here to designate the action of tides and waves upon strand vegetation, and the action of stream and ocean currents in distributing seeds. These factors may play an important part in determining the peculiarities of plant societies, hence the necessity of keeping them in mind.

BIOTIC FACTORS. Two plants cannot occupy the same soil at the same time. The struggle for a foothold in the soil may take place between species of the same kind or of different kinds. Again, the struggle may be between plant societies, as the forest and heath, or forest and prairie. The line along which two societies meet has been called the tension line. Here it is that the struggle is most pronounced. If the other ecological factors remain constant, the tension line does not change. In that case, for instance, the forest does not advance on the heath nor the heath on the forest. But, as will be shown in the discussion of the historical factors, the conditions as a rule are changing constantly. Not only may the struggle be between the forest on the one hand and some other type of plant society on the other, but it may be between different kinds of forests.

The struggle between plants and animals may have an important bearing on the explanation of any given floral region. In civilized communities man has changed the whole nature of the vegetation. His influence is seen where forests are cleared for timber and fuel, or for purposes of cultivation; also indirectly where forest and prairie fires are active. Again in regions where stock is raised trees are damaged or kept from spreading by the ravages of domestic animals. Insect life may also be an important factor in explaining the floral character of a given region.

In concluding this discussion of the ecological factors, it is well to note again that the three great physical media—soil, air, and water—are all influential in bringing about certain plant physiognomies. These, together with the biotic factors, make that variety in the landscape of any region which is shown in the plant societies that are present.

C. **Historical factors.** The third great set of factors that play a part in the understanding of plant associations has been designated historical, for it involves the element of time. It means simply that the geological and physiographic forces have changed and are changing the factors so far considered as to make absolutely necessary a readjustment of plant formations and plant societies to meet the new conditions. Diastrophic movements may submerge large areas of land and thus destroy all terrestrial vegetation or force it to migrate to unsubmerged parts. On the other hand, when there is an addition to the land area a condition is obtained where there can be noted the successive stages in the reclamation of such an area by vegetation. Again, in the last glacial epoch the ice sheet in its advance destroyed vegetation and modified the climate beyond the limits of its advance, so as to bring about an arctic vegetation where there formerly existed a temperate floral formation.

Erosive forces also come into play. The advance and retreat of the ice sheet changed the physiographic features. Drainage lines were dammed up and lakes were formed. It is the belief of glaciologists that the great lakes, at least in part, were formed in this way. Oscillations in the change of the front of the ice sheet changed the levels of lakes and left old beaches, other sand formations, and cliffs, thus bringing into existence new topographic forms and new soil conditions. With the final retreat of the ice sheet the normal processes of water erosion began again. Drainage lines became reestablished, and with the aid of decaying vegetation the lakes began to be filled up. The longer an area of land has been free from the ice sheet, the more nearly have its drainage lines become firmly established. It is evident then that the edaphic conditions in a region recently vacated by the ice will be decidedly different from those that have been exposed to the erosive force of water. The more nearly a region reaches base level the more stable will be the edaphic conditions. The recent work of Cowles[5] on the Chicago region shows clearly the successive stages in the advance toward the climax condition. He was also the first[6] to bring out clearly the dynamic conditions due to physiographic changes. It is evident that the existing plant societies must not be looked upon as fixed, but rather as changing from year to year; sometimes slowly, as in the case of swamps; or sometimes with rapidity, as in the case of dune societies.

II. THE SAND SOCIETIES.

The islands of North Manitou and Beaver at the northern end of Lake Michigan, the adjoining mainland on the Michigan side of the lake, and the southern shore of Lake Superior in the neighborhood of Marquette, Michigan, offer exceptionally good fields for a study of the stages in the life history of the forest societies. North Manitou island, in general, consists of a clay core covered over and added to by sand formations, principally beach and dune. So complex are these in the interior that it is difficult to trace any definite time relations, and no attempt was made to do this. On the south and southeast ends of the island however, where the beaches and dunes are in the process of formation, it is not so difficult to discover the time relations. The northern portion of Beaver island and the mainland in the vicinity of Charlevoix, Michigan, have similar formations. On the southern shore of Lake Superior, while the beaches are present, the dunes are for the most part absent. The beach and dune societies have been so thoroughly studied by Cowles that attention need only be called to the points in his work essential to the understanding of the various stages in the life history of the forest of these regions.

---

[5] COWLES, H. C.: The physiographic ecology of Chicago and vicinity; a study of the origin, development, and classification of plant societies. BOT. GAZ. 31: 73–108, 145–182. 1901.

[6] COWLES, H. C.: The ecological relations of the vegetation of the sand dunes of Lake Michigan. BOT. GAZ. 27: 95–117, 167–202, 281–308, 361–391. 1899. *Idem:* The physiographic ecology of Northern Michigan. Science 12: 708, 709. 1900.

THE LOWER BEACH. The lower beach is defined as that portion washed by the summer waves. There are a number of factors here, any one of which may exclude vegetation. Since the beach is the shore drift in transit, the very movement of the sand or pebbles may prevent plant life. The mechanical wash of the waves would uproot any plants that had obtained a foothold. Again, the border between the land and water presents at one time a xerophytic and perhaps the next moment a hydrophytic habitat. However, in protected places, or where the water is shallow for a distance from the shore, the breaker line thus being distant from the shore, a condition is obtained which may bring into existence a hydrophytic society. Wherever sand is accumulating along the shores in the region under discussion, the lower beach is prominent. With a further recession of the lake it may pass into the middle beach. It is considered, therefore, the first stage in the life history of the forest, for by the action of the waves a soil is made, the first requisite for any forest society.

THE MIDDLE BEACH. The middle beach is that portion of the shore drift in transit only during the winter months. It is consequently free from the waves during the growing season. Here, therefore, is a new land formation in which all the factors which prevent growth in the lower beach are eliminated for the brief space of one growing season. While the hydrodynamic factors have been eliminated, certain of the atmospheric, edaphic, and historical factors are detrimental. Since the former are considered in the initial stages of the upper beach society, they will be discussed under that head. In the short period that this beach is left untouched by the wave action, no plants of any consequence can obtain a foothold. This, together with the sterile soil of sand or pebbles and the extreme exposure to insolation, often prevents the growth of any species. In a few instances the annuals, *Cakile Americana* and *Corispermum hyssopifolium*, and the first year's growth of the biennial, *Oenothera biennis*, are present. If the new land thus made contained an alluvial soil stocked with seeds, one might expect a more or less abundant growth of annuals, though the insolation would still be very great, and would undoubtedly prevent a rich growth. Since the middle beach, by a further recession of the waters of the lake, may become a fossil beach, and thus reach, as will be shown later, a condition more near the forest, it is regarded as the second stage in the life history of the forest.

FOSSIL BEACH. The fossil beach is that portion of the shore beyond the reach of the hydrodynamic factors. In the initial stages the fossil beach is as barren of vegetation as the middle beach, and if in an exposed situation the wind (*fig. 1*) shifts the sand repeatedly, this condition is maintained for a greater or less length of time. If fairly well protected from winds, successive plant societies appear rather rapidly.

The well-known physical and chemical qualities of sandy soils need not be discussed at length here. While the upper layers of sand dry out rapidly, observations seem to show that the lower layers are moist up to high levels. However, the first few layers are extremely dry after a short period of drouth, due to the rapid evaporation from the loose soil. The soil heats up and cools off rapidly, so that the variation in temperature in a short space of time is great, a condition unfavorable to plant growth. Nevertheless, in spite of the strong insolation and dry soil, if sufficient time elapses a definite fossil beach society is obtained. The enumeration of species is not of any consequence. They are at first mostly herbs, both annual and perennial. By their death, and in some instances by the decay of old logs left by storms when the beach was nearer the lake, humus conditions of the soil are gradually obtained. This is at first slow because of insolation. Nevertheless, each year adds its growth of herbs, and even though a greater part is dried out or blown away, in time the better humus condition will bring about the possibility of a higher type of plant society, so the fossil beach society gradually develops into a heath.

HEATH. The heath society is considered, in the normal development, the fourth stage in the life history of the forest. It will be well to keep in mind the changes that make possible the heath. These are the increase in the amount of humus and the element of time. *Juniperus communis*, *J. Sabina procumbens*, *Arctostaphylos Uva-ursi*, *Pteris aquilina*, *Zygadenus elegans*, *Solidago nemoralis*, *Campanula rotundifolia*, and *Comandra umbellata* are some of the characteristic plants of the heath. *Fig. 1* shows a heath at the foot of a coniferous forest on the lake side of a sand dune.

Now for the first time biotic factors assume some importance, though slight. In the first three stages the struggle of plants against adverse physical conditions gave plenty of room for all able to survive. Although the physical conditions are still unfavorable, in places plants like the junipers and bearberry may occupy considerable areas to the exclusion of others. In the open spaces between the individual shrubby plants, however, there is sufficient room for a large number of herbs. These by decay contribute humus to the soil, and since the insolation is not so great as in previous societies, a larger portion of the decaying vegetation is prevented from drying out. Thus as the vegetation increases there is a gradually increasing increment of humus, and this constitutes a condition favorable to a higher type of plant society.

THE CONIFEROUS FOREST. It is not always easy to determine the conifer that first comes to occupy a place in the heath. If conclusions can be based upon a limited number of observations, the jack pine (*Pinus Banksiana*) is the most xerophytic (*fig. 2*). This is followed closely by the red pine (*P. resinosa*) and the white pine (*P. Strobus*) in the order named. This does not mean that anyone of these always appears to the exclusion of all others, though that is sometimes the case (*fig. 2*). Other things being equal, the more xerophytic the conditions the more likely is it that the jack pine will be the predominant tree, and the less xerophytic the conditions the more abundant the white pine. *Fig. 3* is a photograph of a pine forest in which the red pines form a large proportion of the trees. In this forest are a number of white and jack pines. If the succession as given above be correct, it means that this forest is probably a transition between the jack pine society and a white pine society. In the ideal case, then, the succession of predominant species is in the order named. The drier and perhaps the colder the climate up to a certain point, the more likely is this succession to be realized. Thus, in the Marquette region almost pure jack pine forests are found, while at North Manitou island, where the climate is more uniform, the jack pine stage is almost eliminated. Very often the balsam (*Abies balsamea*) (*fig. 1*) and hemlock (*Tsuga Canadensis*) occupy a prominent place in the coniferous forest.

The first stages of the pine forest society are seen in the appearance of a number of trees in the later stages of the heath. For the first time in the normal development of the plant societies the tree has to be taken into consideration. In the tension zone between the heath and forest the trees are more scattered near the heath, and become gradually thicker as the forest is approached. The territory between the trees, where not shaded, is usually occupied by a growth of the heath plants already named. Thus, gradually the pines advance on the heath, and in time come to occupy its territory. In the young pine forest near the tension zone there are often found scattered trees of the white birch (*Betula papyrifera*), oak, and the poplars (*P. tremuloides* and *P. grandidentata*). As the forest reaches maturity, these are usually crowded out, the birch being the last to disappear.

Thus, with time and with the gradual increase of humus, the pine forest society is established. As a rule, the white pine seems to occupy the tension zone between the coniferous and the deciduous forests. If the climate be unfavorable for a higher type of forest tree, however, a stage beyond the white pine forest is not reached. If the forest be not too open, and if surface fires are absent, the deep shade established by the pines means that the edaphic and atmospheric factors have become favorable for establishing the climax forest of the region.

MAPLE, BEECH, AND HEMLOCK FOREST. Beginning with the middle beach we have seen that in each successive society a gradually increasing quantity of humus has been added to the soil, until a white-red pine forest is established. The pines add their quota of vegetable decay to the humus. The xerophytic soil thus becomes more and more mesophytic, and *pari passu* it has become more and more shaded. The humus means that the almost sterile soil of the beach has become richer in organic compounds, and by the aid of fungi and bacteria more nitrates are added. The capacity of the soil to hold water is likewise increased. The better edaphic and atmospheric conditions make a natural nursery for the growth of beech (*Fagus ferruginea*) and maple (*Acer saccharinum* Wang.) seedlings. The white pine does best in the richer soil conditions, but its seedlings require more light than they can obtain in the shade of the forest. As the maple and beech attain maturity, they come to occupy a prominent place in the forest, and a mixed pine-deciduous forest is the result. The broad-leaved deciduous trees produce a still deeper shade, so that if any pine seedlings are able to survive in the pine forest, the increasing shade will finally make it impossible for a new generation of pine trees. The development of beech and maple seedlings, however, is not affected by the shade of the parent trees. In the midst of the deciduous forest isolated white pines are often seen rising above their neighbors, and thus stand as relics of a previous pine forest. A pine starting from a seedling condition with young deciduous trees as a rule never reaches a height greater than that of the trees among which it is growing. At the same time the girth of such a tree is much greater, owing to the better soil conditions, than it would be were it growing among its kind, where it must necessarily grow taller or be crowded out in the struggle for light.

The place of the hemlock in the pine and deciduous forests is a peculiar one. It often composes 10 per cent. of the trees in a white pine forest, and may reach as high as 50 per cent.[7] It seems to be of about the same age as the trees with which it grows, and hence probably started with them. This probably means that its seedlings are able to develop like those of the pines, without being shaded. Yet it often occupies a prominent place in the deciduous forest (*fig. 4*), even when the shade has become so dense as to exclude any chance for the development of white and red pine seedlings. It apparently occupies this position among the maple and beech because its seedlings can endure shaded conditions, although they do not thrive in such situations. Dwarfed young trees fifteen or more years old are often found in the densest shade possible. These develop slowly, until an open place is made by the death of the older trees around them, when they spring rapidly into prominence and occupy a position equal to that of the maple and beech. Like the white pine, the hemlock will flourish in the more xerophytic places, but prefers the deciduous woods and does best in them. The balsam also occupies a position similar to that of the hemlock, although it is seldom present in a mature climax forest. The yellow birch (*Betula lutea*) has a constant place with the beech, maple, and hemlock. It is more plentiful in the Marquette region than farther south, but seldom constitutes more than a small percentage of the total number of trees. The beech is absent in the Marquette region, and the significance of this is not clear. It may be due to the fact that the climate is not favorable for its development. It is present, however, in the northern peninsula east of Marquette.

---

[7] SPALDING, V. M., and FERNOW, B. E.: The White Pine Bull. 22. U. S. Department of Agric., Div. of Forestry. 1899.

The whole interior of North Manitou island (*fig. 4*), except in clearings and undrained areas, is covered with a mature maple-beech-hemlock forest. The presence of seedlings and young trees of these three in abundance and the absence of all other young trees in their shade indicate that the future forest growth will be the same as the present. The climax forest in places reaches nearly to the shore of Lake Michigan, restricting the coniferous and heath societies to very narrow belts. If the present shore line should remain constant, and if the natural succession of plant societies were not interfered with by man, undoubtedly the whole island would in time become completely covered with a deciduous forest save a narrow strip, the last remnants of a coniferous forest, next the water's edge.

The undergrowth in the dense shade of the maples, beeches, and hemlock is scanty. *Taxus Canadensis* and *Mitchella repens* are usually the most abundant. The spring plants are characteristic, but their vegetative period is confined to the leafing time of the trees under which they grow, so that by midsummer only traces of the many forms survive. The loose sandy soil is favorable for creeping underground stems. Lianas are entirely wanting. This is probably due to the lack of sufficient light and heat, for in the open woods farther south the liana habit is common, and as one approaches the tropics the increasing warmth, even in dense shade, favors a luxuriant growth of lianas. Epiphytes, except mosses, liverworts, and lichens growing on the bark of trees, are also absent.

Aspidium spinulosum intermedium, *A. marginale*, *Lycopodium lucidulum*, *L. inundatum*, *Actaea alba*, *Goodyera pubescens*, *Osmorrhiza brevistylis*, *Maianthemum Canadense*, *Monotropa uniflora*, *Corallorhiza odontorhiza*, and *Epiphegus Virginiana* are among the most common plants that occupy a place in these forests.

The humus in the soil is usually variable in amount, but is most plentiful where fallen logs have decayed. Hummocks of soil rich in humus mark places where dead trees when uprooted brought with them quantities of earth. The decaying logs are covered with fungi and mosses. Indeed the soil itself is full of a living mass of hyphæ. The recent researches of Stahl[8] show that mycorhiza is the exception rather than the rule. The rôle that mycorhiza plays is problematic. Some plants, the European beech among them, are entirely dependent upon these root-fungi, for when grown in sterile soil they perish. This seems to indicate that the beech cannot thrive in soil without humus, for its root-fungus is dependent upon organic decay for its existence. In other words, the absence of humus means the absence of mycorhiza, and its absence excludes the beech. Indeed, future investigation may show that a large majority of forest trees and other forest plants have established an obligate mutualistic relation with root-fungi.

THE DUNE SOCIETIES. In discussing the sand societies the conditions favorable to the formation of dunes have been disregarded. Where the wind sweeps across the fossil beach the succession of plant societies is retarded. The extreme exposure to the xerophytic influence of the wind often prevents the presence of plants. Nevertheless, when not too severe, a definite beach society is finally attained. The origin and development of dunes and dune societies have been clearly shown by Cowles.[9] It is only necessary to emphasize the fact here that the plant succession on dunes is similar to that on the beaches, and that in time the climax maple-beech society is reached. *Fig. 1* is from a photograph, showing a fossil beach society in the foreground. On the right is a dune clothed with a coniferous forest. At the base of the dune is a heath encroaching upon the beach. On the landward side of this dune there are indications of the beginnings of a maple-beech forest, and farther inland are dunes which have passed through the first stages into mature climax societies. Dunes clothed with maple-beech forests are also found along the Michigan coast in a number of localities. It is difficult to understand how such a mesophytic plant society is attained, unless it be assumed, as observation seems to indicate, that by capillarity, water may rise from the ground water level to considerable heights in sandy soils.

---

[8] STAHL, E.: Der Sinn der Mycorhizenbildung. Jahrb. f. wiss. Bot. 34 : 539–668. 1900.

[9] Sand dunes of Lake Michigan, BOT. GAZ. 27 : 95 ff.

III. THE CLAY SOCIETIES.

There are greater difficulties in tracing the life-history of clay societies than of sand societies, principally because there is not such a perfect sequence of clay formations at the present time as of sand formations. With the exception of sea-cliffs and clearings, clay soil formations free from vegetation date back to the time of the retreat of the last ice sheet. Sea-cliffs, however, formed by the action of the waves on glacial clay, are a common feature along the shores of Lake Michigan. Here the waves are constantly undermining the cliff, and thus prevent anything more than a transient vegetation. But should the débris at the foot of the cliff become too great for the shore current to transport, or should a recession of the waters of the lake leave a cliff beyond the reach of the waves, the undermining would cease. Here then at the outset is a clay bluff almost free from vegetation.

The reclamation by plant growth begins at once. The first stage in the life-history is represented by herbaceous plants like *Solidago humilis*, *Aster laevis*, *Elymus Canadensis*, *Prenanthes alba*, etc. Later on xerophytic shrubs like *Shepherdia Canadensis* and *Juniperus communis* give a heath-like physiognomy to the bluff. Again, a third stage is reached in the appearance of conifers, poplars, and white birch. These stages are more rapid, for clay soil retains moisture more readily than the sandy soils. The action of humus on clay is exactly the reverse of its effect on sand, for it loosens up the soil and renders it much less soggy than it would be were it free from organic decay. Where the cliff has been long enough freed from the action of the waves, in due time a maple-beech-hemlock condition is the result. Thus, starting with an herbaceous vegetation similar to that on the fossil beach, there is a transition through the heath and coniferous forest to the climax society. Making due allowance for difference in climate, it is probable that all the glacial clay lands in the region under discussion have passed through somewhat similar stages, since they were formed by the action of the last ice sheet. As a rule, where the vegetation has not been disturbed by man, they are clothed with maple-beech-hemlock forests. Where clearings are made, as will be shown subsequently, they rapidly attain the same forest condition if let alone.

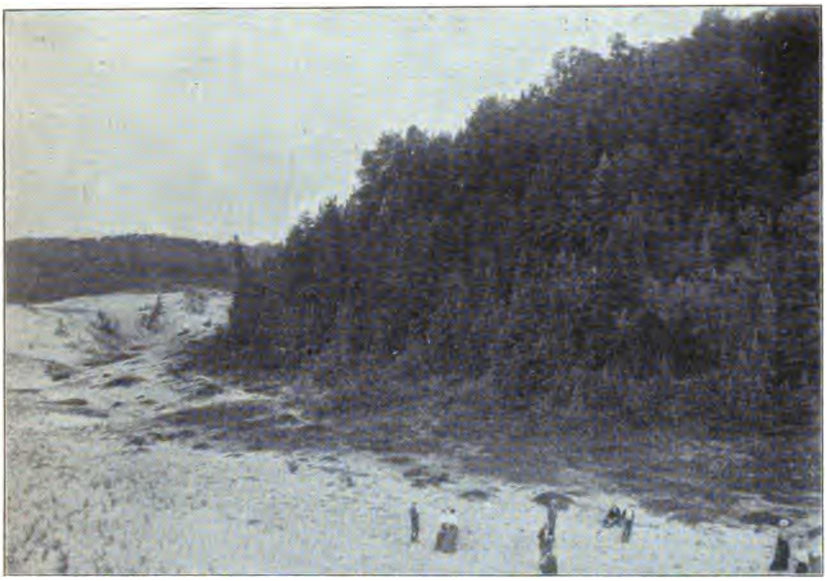


FIG. 1.—The lakeward slope of a sand dune on North Manitou island covered by a forest. Balsam is the most common tree. The undergrowth is very dense, and the deep shade furnishes favorable conditions for the development of maple and beech. The evergreen forest is encroaching on the evergreen heath seen at the foot of the slope, and the latter, in turn, is encroaching on the fossil beach society situated in the foreground.

IV. THE ROCK SOCIETIES.

The pre-Cambrian rocks of the Marquette region furnish an excellent field for the study of the succession of plant societies. The rocks are mostly granites and quartzites. The chemical nature of the rocks seems to have little influence on the ultimate plant society that is obtained, but the ease with which they disintegrate is different, therefore the rapidity of the succession of plant growth is influenced. Other things being equal, granites, because of their heterogeneous structure and consequently differential weathering, will furnish a soil more quickly than the homogeneous quartzite. In the region under discussion the rocks have not only been worn and polished smooth by the action of the last ice sheet, but since then have lain beneath the waters of the former extension of Lake Superior. Indeed, some of them have only recently emerged from the lake. Thus just as there are beach lines of different ages, so there are rock areas of different ages. Other things being equal,

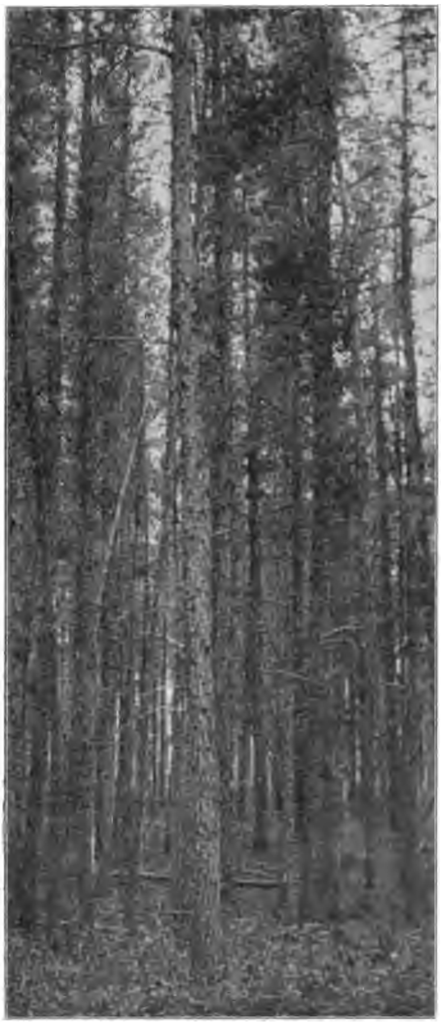


FIG. 2.—Jack pine forest on a fossil beach near Marquette. The absence of undergrowth is due to repeated surface fires.

the longer the rocks have been subject to sub-aerial influences the more nearly they approach the condition of the climax plant society.

On the sand formations at the contact of the lake with the shore the hydrodynamic factors absolutely prevent plant growth. Here likewise, where the rocks dip beneath the lake, there is a zone of no vegetation. However, often within the reach of not too active waves lichens are found. Many lichens need no soil; such are essentially lithophytes and are soil makers. They are fastened firmly to the rocks by holdfasts which secrete acids that aid in disintegrating the rocks on which the lichens grow. Lichens receive moisture from the rain that falls on them, or, when near the water's edge, from the wash of the waves. Between rains they dry and curl up, but are uninjured, for after

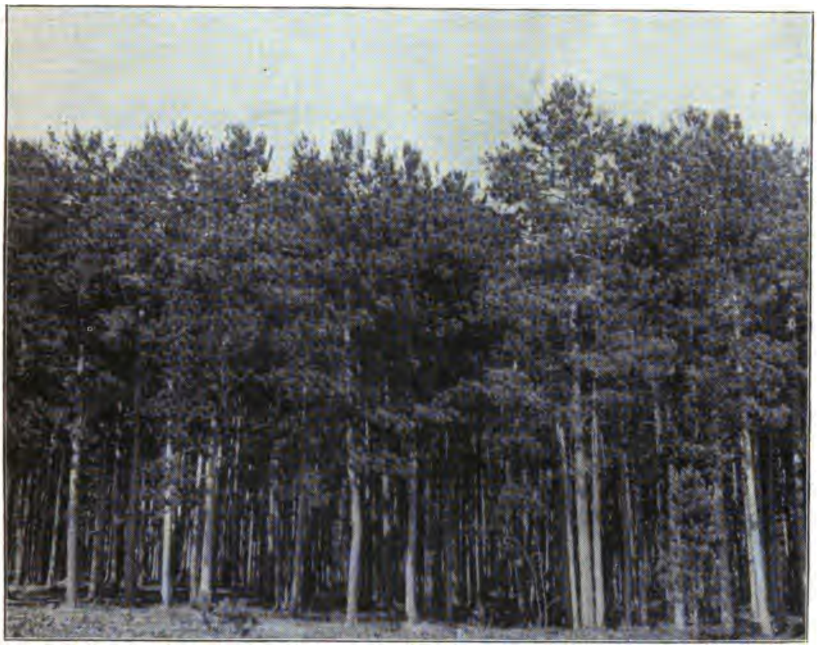


FIG. 3.—Norway pine forest on an old beach near Marquette. This forest also contains a few white and jack pines.

the next rain they are as fresh as ever. Nitrogen compounds are obtained from the rain water or from particles of dust which lodge around them and other requisite inorganic compounds come from the rocks. Thus these pioneers of vegetation, as has been shown by various writers, are able to flourish in the most xerophytic situations. They not only aid in disintegrating the rocks, but by decay furnish humus constituents to the soil, and in these ways, *pari passu*, both organic and inorganic soil is made.

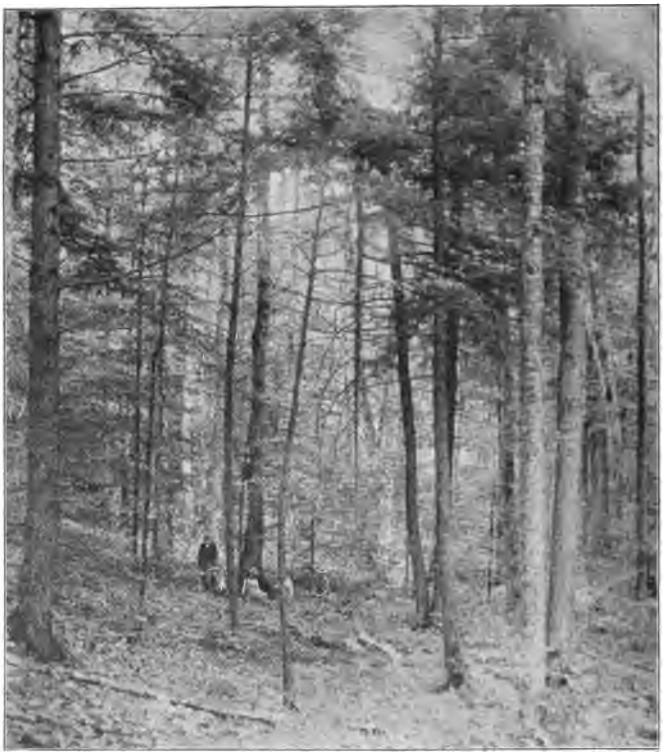


FIG. 4.—A maple-beech-hemlock forest in sandy soil on North Manitou island. The undergrowth consists principally of maple, beech, and hemlock seedlings and young trees; also *Taxus Canadensis* and *Mitchella repens*. The young trees indicate that the next generation of trees will be the same as the present.

If the lichens be on not too steep a slope they will in themselves furnish soil enough to maintain a higher form of plant life. Xerophytic mosses gain a foothold as soon as a slight soil is made. These, too, by decay aid the lichens in forming a soil that will support still higher forms. *Fig. 5* shows such a society. It is even possible, in time, without the aid of inorganic processes of weathering to establish a soil capable of supporting a tree vegetation. However, inorganic processes of weathering are going on continually. Changes of temperature, etc., crumble the rocks and form crevices in which soil lodges. Since most of

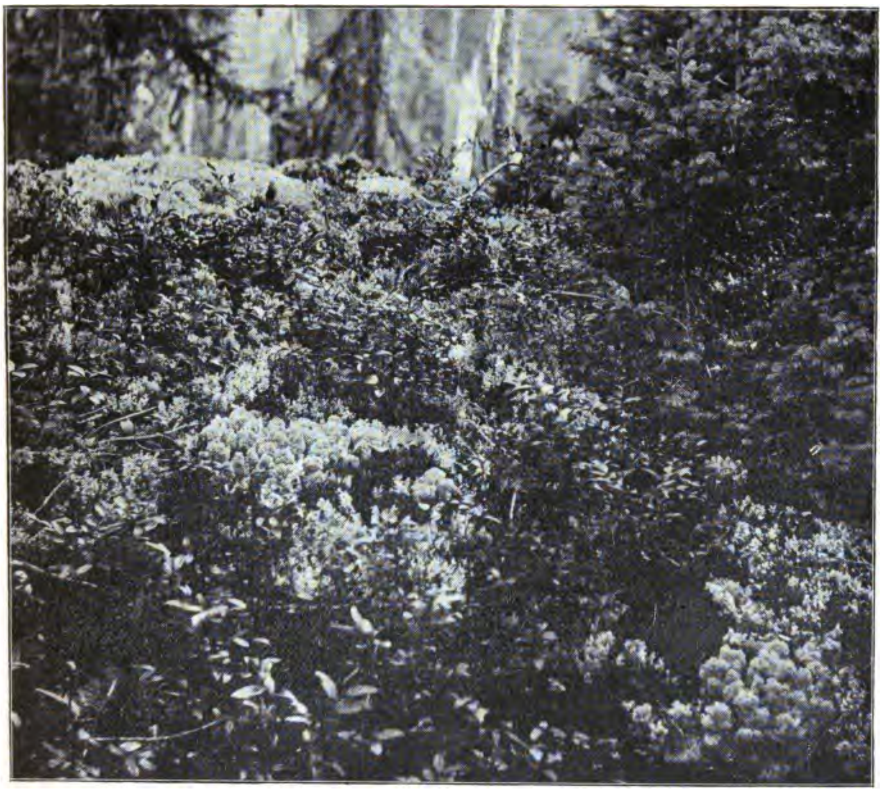


FIG. 5.—A granite rock covered by the lichen *Cladonia rangiferina*, moss, and herbaceous plants. To the right are conifers growing in the crevices of rocks.

the rock surfaces are not level, the soil made by lichens and mosses is washed into the crevices or into hollows made by the action of ice or water erosion. At once a herbaceous and shrubby vegetation springs up. Plants like huckleberries, goldenrods, *Potentilla tridentata*, *Campanula rotundifolia*, and the bearberry gain a foothold in the crevices. These are followed by arbor vitae (*Thuja occidentalis*), the junipers, and the pines. *Fig. 6* shows a rocky island in a bay near Marquette. At a distance it looks barren of vegetation, but a closer view (*fig. 7*) shows that it is not altogether destitute of plant life. *Fig. 8* is from a photograph of a larger island near by which shows a much higher type of vegetation, for here are found red and white pines. The weathering process is greatly aided by the prying action of roots. *Fig. 9* shows a red pine whose roots have split and raised a granite rock.

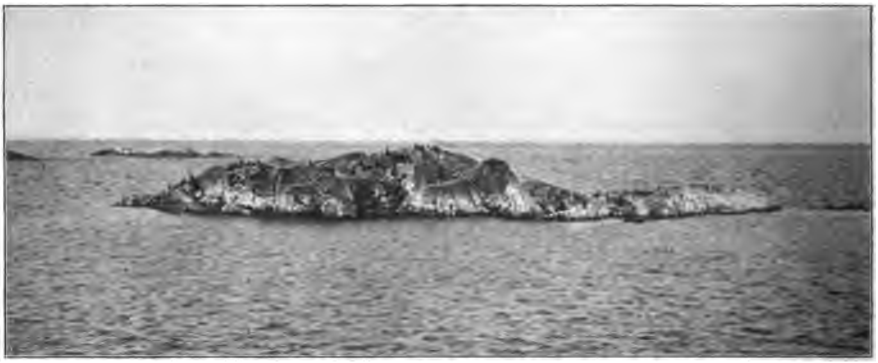


FIG. 6.—A granite island in Lake Superior near Marquette. At a distance it appears destitute of plant growth.

One of the noticeable features of rock vegetation is its variety. Within the limits of a few square rods miniature representations of all the great plant societies are found. Near a *roche moutonnée*, as smooth and as barren of vegetation as the day the ice sheet left it, is a small depression containing a swamp, in which sphagnum moss and the cranberry are found growing. Near by is a lichen society; this may grade into a heath such as is shown in *fig. 5*, and this in turn may border on a small group of pines.

As in the sand and clay series, the mesophytic forest is not reached until first preceded by a coniferous forest. The coniferous forests on the rocks are at first very open, but ultimately the gaps are filled up, sometimes with birch and poplars, and thus a condition is obtained for the maple-hemlock forests. Some rock hills near Marquette illustrate these points. *Fig. 10* is a view from Sugar Loaf. The top of this hill is almost barren of vegetation. Obviously this would be the case, for the soil that is formed descends to lower levels; in the case of steep

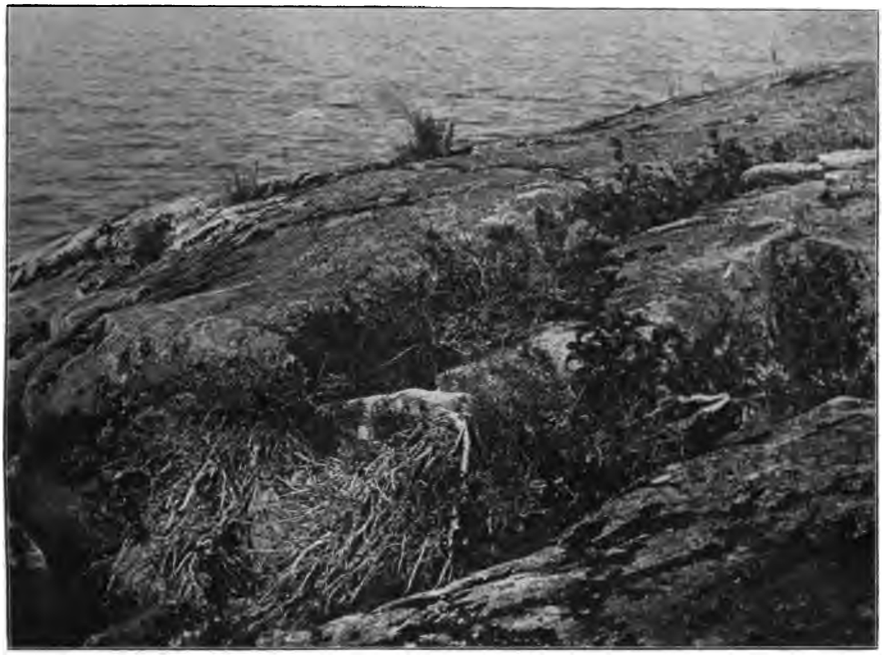


FIG. 7.—A near view of a portion of the island shown in *fig. 6*. On the faces of the rock are shown lichens and mosses. In the crevices are a number of herbaceous and woody plants; among them are goldenrods, poplar, arbor vitae, huckleberry, ninebark, Juneberry, wild red cherry, *Campanula rotundifolia*, and *Potentilla tridendata*.

slopes gravity alone is sufficient, while on all slopes the transporting power of rain water comes into play. Usually at the foot of the hill and sometimes well up the slope the conditions are favorable for the climax society. Other hills (*fig. 17*) farther in the interior are completely covered with pine and deciduous forests.

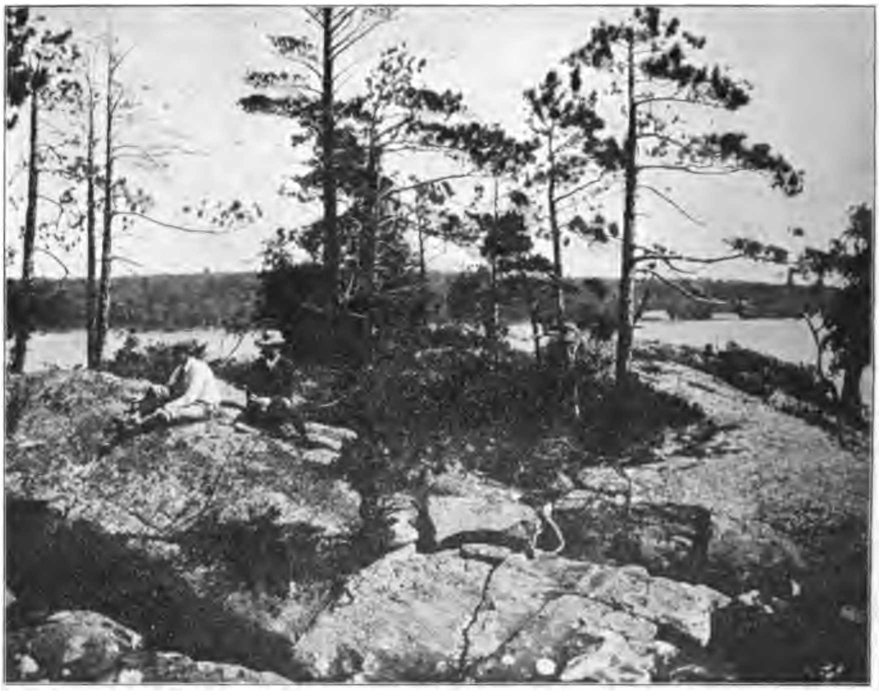


FIG. 8.—Portion of an island near the one shown in *figs. 6* and *7*. Here the vegetation is further advanced. Besides lichens, etc., white and Norway pines are found.

V. THE SWAMP SOCIETIES.

One of the most characteristic features of a young glacial topography is the large number of lakes. In general these may be divided into two classes according to their mode of origin. One class is due to the action of the ice sheet. Depressions may be made directly by the moving ice, or glacial deposits may dam up drainage lines. A second and subsequent class of lakes is made by bars cutting off lagoons from the larger lakes, or by spits formed across their embayments. Both classes have a similar life-history. Some find outlets and ultimately pass out of existence through the normal stages in the life-history of a river. A larger number, however, never find outlets, but are silted up by the wash of the surrounding soil, and by the accumulation of vegetation. Thus swamps are formed, and since they may represent a stage in the life-history of the forest they deserve treatment here.

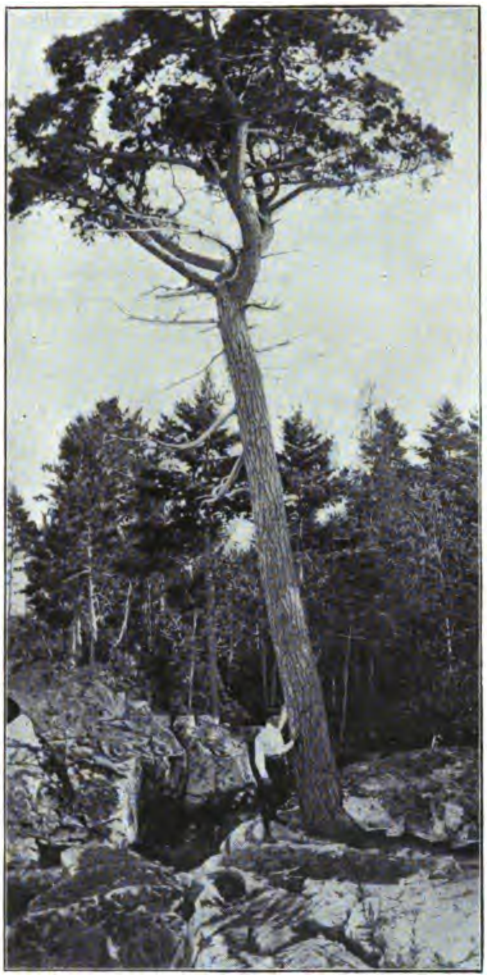


FIG. 9.—A Norway pine growing from a crevice in granite; the rock has been cracked and uplifted by the growth of a root.

The zonal distribution of plants in swamps is one of the stock illustrations of ecologists, so that development of the various zones need only be mentioned briefly. Most swamps start as ponds or lakes, in which water lilies and other pond plants dominate. On the borders of the pond sedges appear; these, by their decay, build up a soil, and thus prepare the way for the next zone, the Cassandra-sphagnum vegetation. The sedges encroach farther on the original lake. The Cassandra-sphagnum zone makes conditions possible for a tamarack-spruce zone (*fig. 11*). Thus each successive zone is pushed farther and farther toward the center. Finally the lily center disappears, and then successively the sedge and Cassandra zones, until a tamarack forest may come to occupy the whole territory.

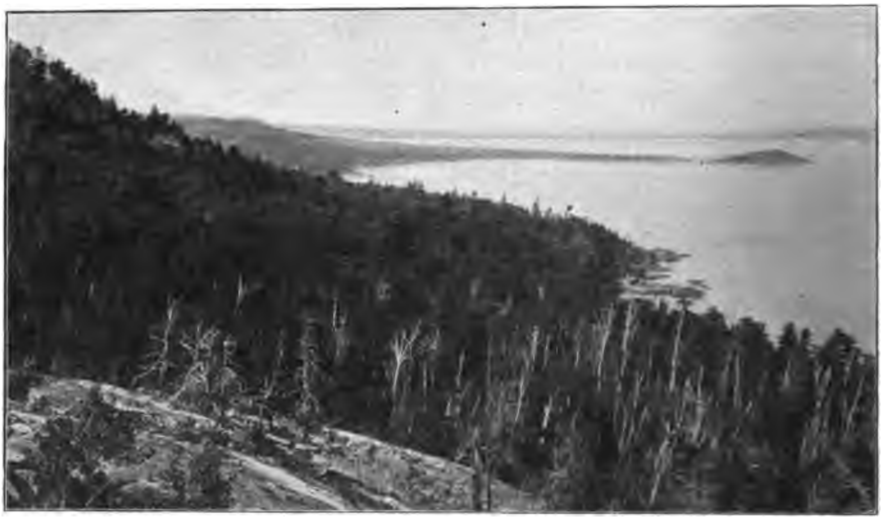


FIG. 10.—A general view of granite rock vegetation as seen from a granite hill (Sugar Loaf) near Marquette. On the margin of the lake the rocks show the first stages in the life-history of a forest. As the foot of the hill is approached the vegetation becomes more and more mesophytic until a mixed conifer and deciduous forest is attained. Probably in places this condition is reached more rapidly because of the presence of glacial drift. At the top of the slopes the xerophytic condition of the lake border is again attained.

Attention has already been called to the probable factors unfavorable to a high development of plant life in these swamps. These are due in the main to undrained conditions. The accumulation of humic acids may cause, osmotically, a drying-up effect. Insufficient aeration of the soil prevents a healthy growth of the root system of highly organized land plants, and also bars the presence of nitrifying bacteria. These probably bring about the xerophytic structures of plants so commonly seen in hydrophytic habitats.

The areas around the swamp, whether clay, sand, or rock, have been undergoing their normal changes, so that the swamp is eventually surrounded by a forest. The swamp is finally built up high enough above the water level to permit a higher type of tree to occupy the area. Thus the tamarack is gradually crowded out, and a climax forest is the final stage.

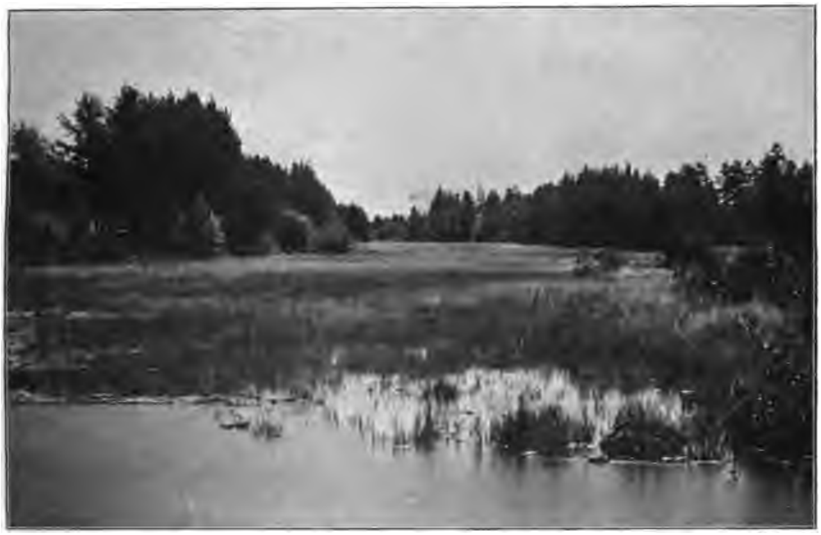


FIG. 11.—A lagoon cut off from Lake Superior by a beach line, resulting in an undrained swamp. In the foreground is seen a portion of the original lagoon; back of this is the sedge vegetation, and near the conifers is a Cassandra zone. The conifers are mostly tamaracks (*Larix Americana*).

The life-history is not always as indicated above. The swamp may become partially drained, but still be too wet to support the highest tree society. In that case the abor vitae gradually replaces the tamarack. Associated with the arbor vitae are the ash (*Fraxinus* sp.), the balsam, the white pine, and the yellow birch. Gradually, however, the arbor vitae swamps give away before the encroaching mesophytic forests. *Fig. 12* shows a hemlock-maple forest bordering an arbor vitae swamp. In wet springy soils the arbor vitae forest is also found. *Fig. 13* shows a young forest in such a situation.

VI. CLEARING SOCIETIES.

Thus far what has been called the normal life-history has been traced. The influence of human agencies, with few exceptions, has been disregarded. By far the greater number of areas studied show unmistakable signs of the devastating influence of man, though less so on the islands visited than on the mainland. These clearing areas cannot be disregarded if a complete history of forest development is to be written. At first the difficulties of getting any order out of the tangle seemed insurmountable, and the notes were usually headed "clearings, conditions artificial." The literature on the subject of plant succession in clearings is confusing. It consists, as a rule, of records of isolated observations without any attempt at correlation. That there is some solution to the problem was the writer's firm belief, and after collecting a large number of notes the study began to yield results.

If the factors controlling the normal development as given above are correct, they ought to dominate in the clearing societies. With two exceptions, the stages observed in the development of these clearing societies are represented in the normal history. These exceptions are the "fireweed" and the poplar-birch societies. To explain these it was found necessary to give prominence to the fact that some plants migrate more easily than others.

If a deciduous forest be destroyed and burned over so that the surface débris is partially reduced to ashes, it will usually be found that the humus conditions of the soil are then reduced toward, but not necessarily to the conditions obtained in the heath. The equilibrium that had been established has been disturbed, and other things being equal all plants will have an equal chance provided their seeds are present. Shade plants, however, including young plants of beech and maple, are excluded because the insolation is great. Some few plants that seem to prefer more xerophytic conditions likewise will not thrive. Then the struggle is narrowed to those plants that can endure strong insolation, that prefer tolerably good edaphic conditions, and whose seeds are present. It is obvious that those plants in the neighborhood that have the lightest seeds will have the largest representation of seeds on the ground first, and of these the most rapid growers will prevail the first year or two. The so-called "fire-weeds" meet the requirements best. *Epilobium angustifolium*, *Erigeron Canadensis*, and certain goldenrods spring at once into an occupancy of the field, and there is given a "fire-weed" physiognomy to the clearing (*fig. 14*).

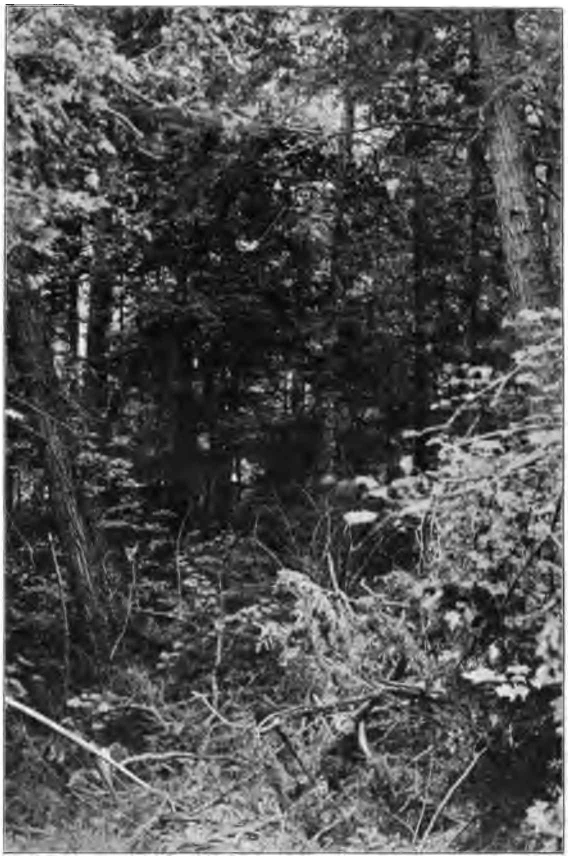


FIG. 12.—A hemlock-maple forest bordering on an arbor vitae swamp. The tangled growth of the arbor vitae swamp is seen in the foreground. The hemlocks are encroaching on the arbor vitae.

The poplars (*P. tremuloides* and *P. grandidentata*) and the white birch are the trees which have seeds adapted for rapid migrations, and are also rapid growers. Because they are perennial, and can thus get an early start each year after the first, they soon overtop the fireweeds and gradually shade them out. *Ostrya Virginica*, *Prunus Pennsylvanica*, *P. serotina*, and *Quercus rubra* are in some places associated with the poplars and birches.

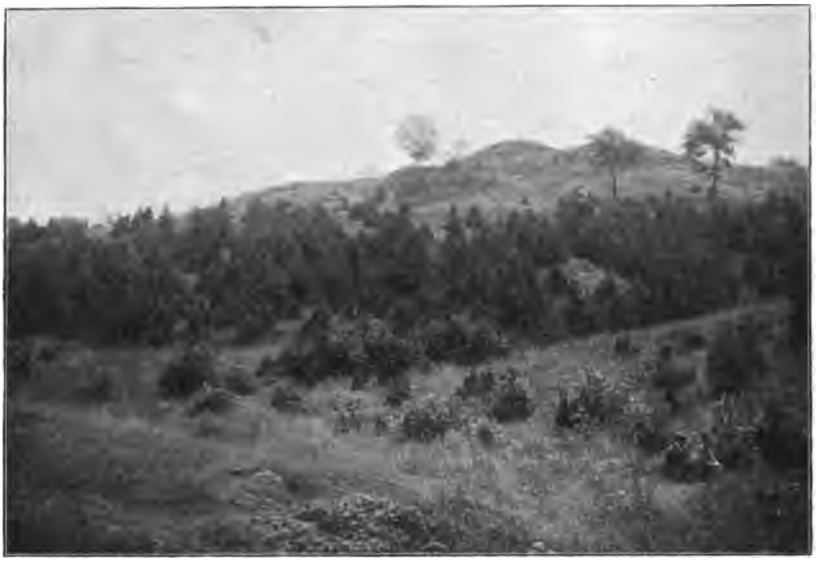


FIG. 13.—A spring hillside with young growth of arbor vitae. The hill in the background has been cleared of a maple-hemlock forest and is used for a pasture.

In the absence of pine trees in the vicinity to furnish pine seeds, this poplar-birch society is maintained until deep shade conditions are again obtained for the growth of the maple-beech seedlings. Then, just as in the normal development the pines are replaced by the maples and beeches, so in the clearing development the poplar and birches are likewise replaced. The poplars go first, then usually the birch and hornbeam, and finally the cherry trees drop out.

If, however, pine trees in the vicinity of a clearing can furnish seeds, the pines occupy a place in the life history. The more unfavorable the humus conditions up to a certain limit, the more likely is the clearing to have a pine aspect. The humus in the soil may be so reduced as to be incapable of supporting a poplar-birch growth. *Fig. 15* shows a young jack pine growth.

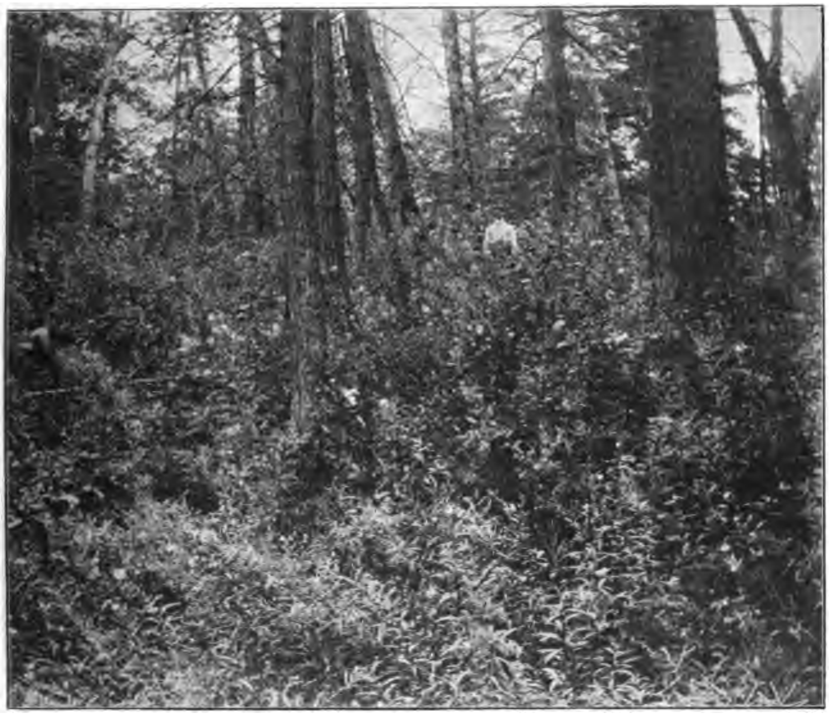


FIG. 14.—A hemlock-maple forest destroyed by fire. The rich growth of fireweed (***Epilobium angustifolium***) indicates the first stage in the life-history of a second-growth forest.

In this repeated fires have probably so reduced the humus conditions of the soil that the most xerophytic of the pines alone is able to gain a foothold. If favorable for the presence of both pine and poplar-birch growth (*fig. 16*), the pines in time overtop the poplars and birch, until a condition corresponding to the normal life-history is attained, viz., a pine society preceding the maple-beech society.

It can be seen readily that it is possible to obtain all stages of reduction between mesophytic and xerophytic conditions. This depends on what stage in the normal life-history is attacked by the fire, and on the intensity or entire absence of subsequent fires. Thus all possible combinations are represented. *Fig. 17* shows a maple-hemlock forest that has been nearly destroyed by fire. This is situated on the slope of a quartzite hill, and had probably reached the climax condition. In places the fire has left remnants of the forest, and even where the trees are destroyed certain geophilous forest herbs like *Clintonia borealis* have maintained themselves in the shade of half burned logs, while near by fireweeds, poplars, and pines are found. *Fig. 18* shows an almost pure birch forest. Not far away, however, are

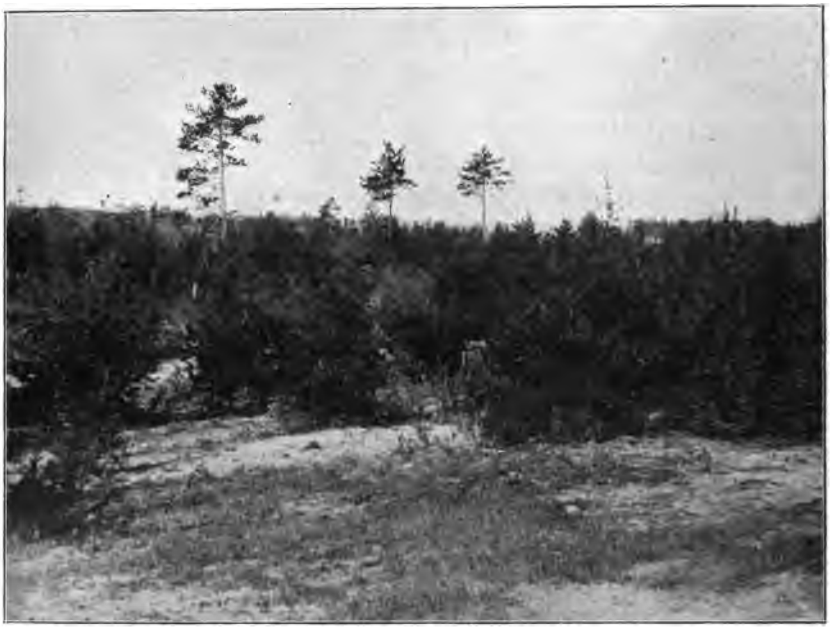


FIG. 15.—A young jack pine forest on a fossil beach near Marquette. The humus content of the soil has been much reduced by insolation and repeated fires. The undestroyed Norway pines in the background probably indicate that the beach had formerly attained the Norway pine stage in the life-history series.

found poplars mixed with the birch. In this neighborhood stumps of pines indicate the former forest. In places repeated fires have reduced the area to heath conditions. This is shown by a number of heath plants like *Pteris aquilina*, *Gaultheria procumbens*, *Cladonia rangiferina*, etc. The presence of few seed-producing pines in the neighborhood will probably account for the absence of many pine seedlings.

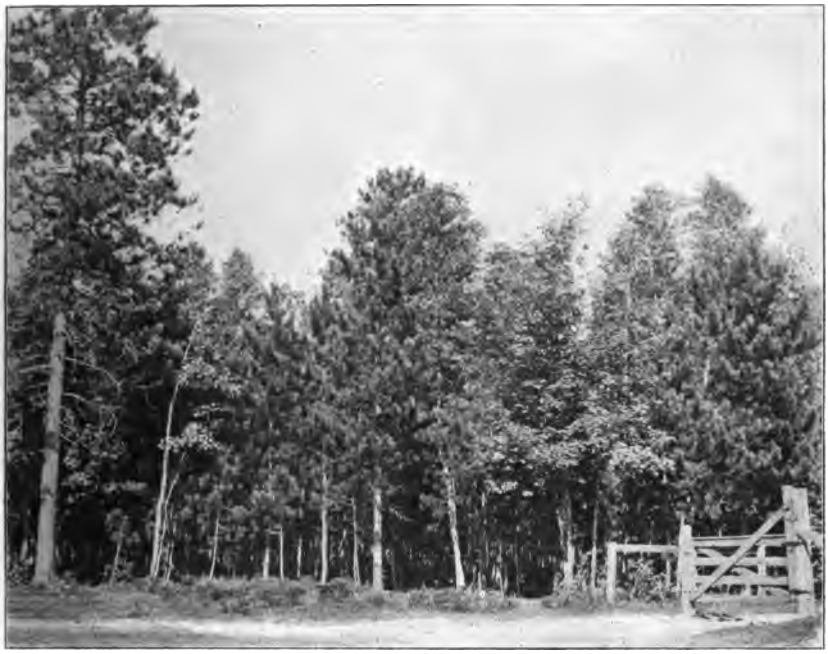


FIG. 16.—A second-growth forest of pines and poplars on a fossil beach near Marquette. The pines are slowly gaining ascendancy over the short-lived poplars and these will in time disappear.

Thus, no matter how far toward the first stage in the life-history a forest is reduced, if not interfered with by human agencies, ultimately the climax forest society is reached, but not without first having passed through a pine or a poplar-birch stage. A maple forest was never observed to follow a maple forest except when the stools of a cleared forest are capable of producing sprouts. These may in time reach tree dimensions, though usually not before a considerable number of pines, birch, or poplars spring up between them.

Thus it will be seen that if human agencies should cease to operate, all classes of topographic forms will ultimately come to be clothed with the climax forest growth. There is no reason why even the jack pine barrens may not in time reach this state. It must be remembered that these are late topographic features, or are reduced by repeated burnings to a soil poor in humus.

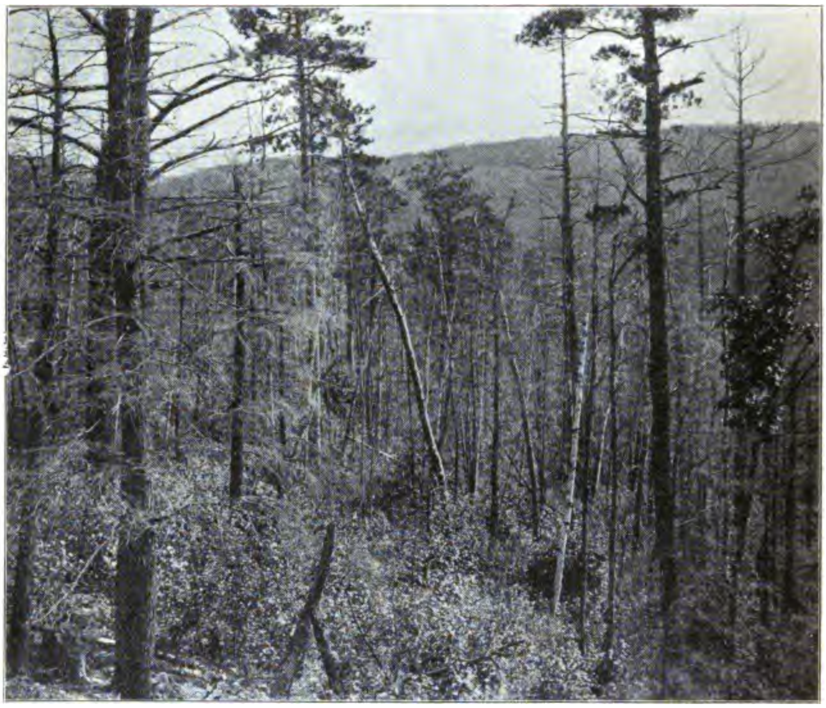


FIG. 17.—A partially destroyed hemlock-maple forest on the slope of a quartzite hill (Mt. Mesnard) near Marquette. The forest had attained the climax stage in the life-history series.

VII. CONCLUSIONS.

The life-history of the vegetation of four sets of physiographic formations has thus been traced. It has been shown that in each series the climax plant growth is a deciduous-hemlock combination. These physiographic formations have been treated separately because usually they are distinct from one another. In some instances, however, clay is mixed with rock débris or underlies the sand. The only effect such a mixture has is to hasten the succession of stages, for the advance toward the climax is more rapid on clay than on other soils. Principally for this reason the clay soils on the whole are already covered with the climax forest. In many instances the sandy soils have likewise attained the last stage in the life-history. Especially is this so where free from the influence of man as on

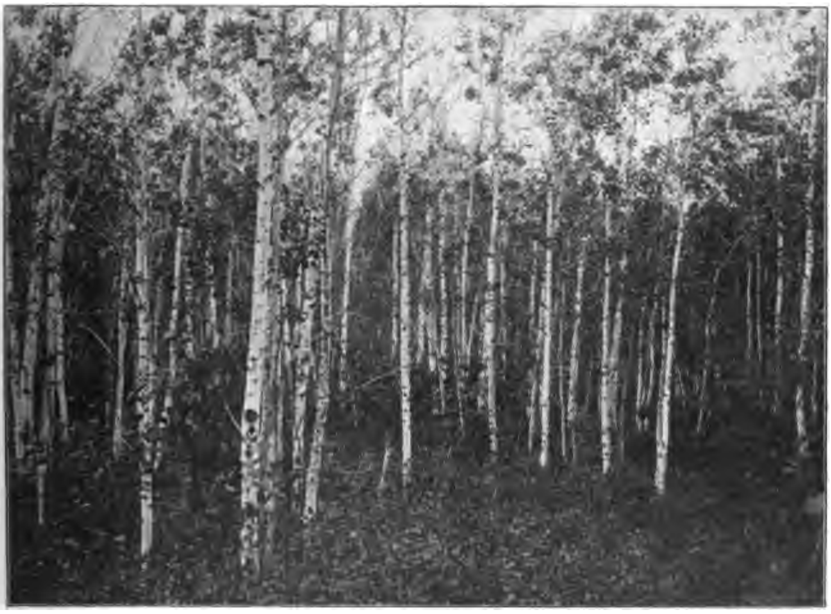


FIG. 18.—A white birch clearing growth on a fossil beach near Marquette. The undergrowth consists of *Pteris aquilina*, *Diervilla trifida*, etc.

North Manitou island. But the succession of plant societies is much slower on sand than on clay soil, hence the prevalence of pine forests on the former. The reasons for believing that ultimately these pine forests will give way to the deciduous have already been given.

It is the belief of the writer that with some modifications the principles brought out in the foregoing pages will hold for all regions climatically capable of supporting a tree vegetation. The region under discussion is physiographically young. If the terms of physiography be adopted for ecology, a region having scanty vegetation may be considered young, while from this there will be all stages through maturity to old age, viz., a mesophytic climax forest. It would appear to the casual observer that northern Michigan is a region physiographically young and ecologically old. But no inconsiderable portion of the area of both Michigan and Wisconsin is occupied by swamps and lakes (including the great lakes). These will remain hydrophytic and hence ecologically young until filled up or drained. This condition is not attained until the region reaches maturity. The whole region, from an ecological standpoint, therefore, cannot reach maturity until it does so physiographically. Thus the development of the forest is in a measure held back until the normal physiographic processes extinguish the swamps and lakes. When these are eliminated, the region will reach old age from the vegetation standpoint much sooner than it does physiographically, because the climate is favorable for the extension of mesophytic forests into altitudes which would otherwise support only a xerophytic society.

In an area where the climate is more severe for tree growth the life-history stages are less rapid, for even though the region may be nearer base level the climax stages are more restricted. For example, Cowles[10] has shown that in the Chicago region, as a rule, the river bottoms contain the mesophytic plant societies, while the clay hills have only attained a semi-mesophytic forest of oaks and hickories. Such clay hills in northern Michigan are usually covered with the climax forest.

---

[10] BOT. GAZ. 31 : 88 ff. 1901.

Again, as one approaches the semi-arid regions of the West, he will observe that the forest growth on the hills becomes less and less mesophytic until finally it gives way altogether to the prairie society. At the same time, the river bottom forests also become less mesophytic and more restricted to the banks of the streams. Ultimately, they, too, in the region of the great plains pass from existence and the prairie reaches to the very margin of the drainage lines. The writer has made some studies at various places in Kansas in reference to these points, and it is his intention to discuss them in full in a future paper on the ecological relations of prairie and forest.

THE UNIVERSITY OF CHICAGO.

3 2044 102 819 331